



Contract theory for the evolution of cooperation: The right incentives attract the right partners

Marco Archetti

Department of Organismic and Evolutionary Biology, Department of Economics, Harvard University, Cambridge, MA, USA

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ABSTRACT

Partner choice is a critical stage of many biological interactions, from mating to cooperation. When the quality of the potential partners is unknown, one way to choose is to rely on signaling: costly signals can reveal the quality of the sender and allow the receiver to choose. In some cases, however, signaling (or an active choice based on signals) is not possible, for example in the initiation of the symbiosis between the squid *Euprymna scolopes* and the bioluminescent bacterium *Vibrio fischeri*. How is partner choice possible in this and other similar cases? I show that in a game with asymmetric information without signaling, imposing a deliberate cost for establishing the interaction allows the non-informed individual to attract the right partner if the cost induces only high quality individuals to accept the interaction. Furthermore, imposing different costs and rewards may induce the informed individuals to screen themselves according to their types, and therefore allow the non-informed individual to establish an association with the correct partners in the absence of signaling.

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1. The problem

1.1. Partner choice

How to choose among potential partners when their quality is unknown? In many pairwise interactions one party has relevant information (for example about his own quality) that the other party does not have. Consider mate choice: in many species females choose males (Andersson, 1995), but they cannot observe their quality directly. While females prefer males of good quality, males would find it profitable to mate irrespective of their quality, therefore they have an incentive to reveal their real quality only if they are good, and to pretend they are good if they are not. How can a female tell a good quality male from a bad quality one? The problem of partner choice (Bull and Rice, 1991; Noë and Hammerstein, 1994; Sachs et al., 2004) is not restricted to sexual selection; it is relevant in any situation in which information is asymmetric.

1.2. Signaling

One way to solve the problem of asymmetric information is by signaling: if the signal has a cost, only good quality individuals will find it profitable to advertise their quality, therefore the signal will be honest. Signaling theory is well known in the context of mate

choice and is relevant to other cases of partner choice. In fact it was introduced initially in economics by Spence (1973) and verbal arguments had been put forward already by Veblen (1899). It was introduced in evolutionary biology by verbal arguments by Zahavi (1975) and formal models by Grafen (1990) and others, and a vast literature on signaling exists (Searcy and Nowicki, 2005; Maynard Smith and Harper, 2003). But what happens when signaling is not possible?

1.3. Partner choice without signaling?

Consider the mutualism between the bioluminescent bacteria *Vibrio fischeri* and the squid *Euprymna scolopes*, one of the most well studied symbioses (Ruby and McFall-Ngai, 1999; Small and McFall-Ngai, 1999; Visick and Mcfall-Ngai, 2000; Visick et al., 2000): the bacteria produce light for the squid while the squid provides shelter for the bacteria. Both luminescent and non-luminescent bacteria exist, and bacteria cannot signal their quality (they are not visible and luminescence occurs only inside the squid), therefore squids are not able to tell good (luminescent) from bad (non-luminescent) bacteria in advance. And yet only luminescent bacteria are normally found in the light organs of the squid. How does a squid manage to interact only with the luminescent bacteria and avoid the non-luminescent ones? Other examples exist in which the informed individual cannot signal or the non-informed individual cannot choose. For example, how do ant-plants recruit only mutualistic ants? In general, is partner choice possible in the absence of signaling?

E-mail address: archetti@fas.harvard.edu

1.4. A cost for entry

The idea of this paper is that there is a solution to the problem of partner choice that does not require signaling. The non-informed individual (the squid for example) can impose a cost for entering the interaction that will lead the possible partners (the bacteria) to screen themselves according to their own interest: if entering the interaction is too costly for low quality individuals (non-luminescent) but not for good quality (luminescent) individuals, then only high quality individuals will find it profitable to enter. This strategy, imposing a cost for establishing the interaction, can induce partners of unknown quality to screen themselves according to their own quality, even though the non-informed individual neither observes quality nor any signal.

2. The contract game

Consider the following game. One individual (the principal) invites another (the agent) to carry out an action; the action requires a cost by the agent and produces a benefit for the principal; the principal pays a reward to the agent. Agents can be of two types x : high ($x=Q$) or low ($x=q$) quality, chosen by nature, known to the agent but unknown to the principal. Agents cannot signal their type. Principals cannot choose the reward based upon the quality or the actions of the agent; instead, the principal can only set up certain fixed conditions (a reward offered and an effort required) that agents of unknown quality can only accept or reject. Our question is: is it possible for a principal to design the right costs and rewards to attract only Q agents?

Agents can choose to remain free-living or engage in the interaction, based on their own quality. Agent strategy \mathbf{a}_i is defined by the vector $\mathbf{a}_i=[a_i(Q),a_i(q)]$, where $a_i(x)$ is the probability that when the agent is of quality x , he enters an interaction with the principal. The four possible pure strategies \mathbf{a}_i are as follows:

- $\mathbf{a}_1=[0, 0]$ (never enter).
- $\mathbf{a}_2=[1, 0]$ (enter only if Q).
- $\mathbf{a}_3=[0, 1]$ (enter only if q).
- $\mathbf{a}_4=[1, 1]$ (always enter).

Principals can be demanding or non-demanding. Principal strategy p_j is defined by the probability that the principal imposes a cost on the agent to enter the interaction. The two pure strategies are as follows:

- $p_1=1$ (demanding).
- $p_2=0$ (non-demanding).

The fitness of agent strategy \mathbf{a}_i is

$$W(\mathbf{a}_i) = \sum_{j=1,2} f_{p_j} \sum_{x=q,Q} f_x \{ a_i(x)[p_j(1-\alpha_x) + (1-p_j)(1)] + [1-a_i(x)]\phi_A \}$$

The fitness of principal strategy p_j is

$$W(p_j) = \sum_{i=1,4} f_{\mathbf{a}_i} \sum_{x=q,Q} f_x \{ a_i(x)[(1-\pi_x)] + [1-a_i(x)]\phi_p - \delta p_j \}$$

where f_{p_j} is the frequency of principal strategy p_j , $f_{\mathbf{a}_i}$ is the frequency of agent strategy \mathbf{a}_i , f_x is the frequency of agents of quality x , α_x is the cost paid by an agent of quality x interacting with a demanding (p_1) principal ($\alpha_q > \alpha_Q$), π_x is the cost for any principal interacting with an agent of quality x ($\pi_q > \pi_Q$), δ is the cost for being demanding for a principal (p_1), and ϕ_p and ϕ_A are the reservation utilities (the payoffs for free-living) for principals and agents, respectively. A principal prefers to interact with a Q agent than being free-living

($1-\pi_Q > \phi_p$) and prefers to be free-living than interacting with a q agent ($1-\pi_q < \phi_p$).

2.1. The simultaneous game

Consider first the game in which agent and principal move at the same time (or at different times without observing each other's moves). With $f_{p_1}=1$,

$$\begin{aligned} W(\mathbf{a}_1) &= \phi_A \\ W(\mathbf{a}_2) &= f_Q(1-\alpha_Q) + f_q(\phi_A) \\ W(\mathbf{a}_3) &= f_Q(A) + f_q(1-\alpha_q) \\ W(\mathbf{a}_4) &= f_Q(1-\alpha_Q) + f_q(1-\alpha_q) \end{aligned}$$

therefore it is easy to see that \mathbf{a}_2 (enter if Q) is a dominant strategy when $1-\alpha_Q > \phi_A$ and $1-\alpha_q < \phi_A$. With $f_{p_2}=1$

$$\begin{aligned} W(\mathbf{a}_1) &= \phi_A \\ W(\mathbf{a}_2) &= f_Q(1) + f_q(\phi_A) \\ W(\mathbf{a}_3) &= f_Q(\phi_A) + f_q(1) \\ W(\mathbf{a}_4) &= 1 \end{aligned}$$

therefore it is easy to see that \mathbf{a}_2 (always enter) is a dominant strategy if $\phi_A < 1$.

If $\delta=0$ (there is no cost for being demanding), principal strategies are neutral, irrespective of the type of agents. If $\delta > 0$ (there is a cost for being demanding), however, principal strategy p_2 (non-demanding) dominates p_1 . Therefore (\mathbf{a}_4,p_2) ("always enter", "non-demanding") is stable if $\delta \geq 0$, while (\mathbf{a}_2,p_1) ("enter if Q ", "demanding") is stable only if $\delta=0$. In summary, mutualism can be stable in the simultaneous game only if there is no cost for being demanding for the principal; even in this case whether this (\mathbf{a}_2,p_1) or the alternative (\mathbf{a}_4,p_2) equilibrium will evolve depends on the initial conditions of the system. Fig. 1 shows a simplified version of this game with only two agent strategies.

2.2. The sequential game

Consider now the sequential version of the same game, in which the principal moves first (Fig. 2). As before, if the principal is demanding (p_1) agent strategy \mathbf{a}_2 ("enter only if Q ") is stable if

$$1-\alpha_q < \phi_A < 1-\alpha_Q \tag{1}$$

while if the principal is non-demanding (p_2) agent strategy \mathbf{a}_4 ("always enter") is always stable (if $\phi_A < 1$). Now, since with agent strategy \mathbf{a}_4 $W(p_2)=f_q[1-\pi_q]+f_Q[1-\pi_Q]$ and with agent strategy \mathbf{a}_2 $W(p_1)=f_q[\phi_p]+f_Q[1-\pi_Q]-\delta$, we can reason by backward induction that \mathbf{p}_1 ("demanding") is the best strategy for the principal when $W(p_1) > W(p_2)$, that is when

$$\delta < f_q[\phi_p - (1-\pi_q)] \tag{2}$$

Therefore (1) and (2) are the conditions for the stability of the following strategy in a sequential game in which the principal moves first: the agent plays "enter only if Q " if the principal is demanding ($\mathbf{a}_2|p_1$) and "always enter" if the principal is non-demanding ($\mathbf{a}_4|p_2$); the principal plays "demanding" (p_1). We can define an agent strategy using the matrix $\mathbf{s}_{i,j}=[\mathbf{a}_i|p_j]$; the conditional agent strategy described above corresponds to $\mathbf{s}_{2,4}=[[1,0][1,1]]$; the strategy "never enter" corresponds to $\mathbf{s}_{1,1}=[[0,0][0,0]]$, and "always enter" corresponds to $\mathbf{s}_{4,4}=[[1,1][1,1]]$ (while this notation is useful to define conditional strategies, with one principal strategy j fixed in the population the game reduces to the four-strategy game described so far).

The replicator dynamics (Figs. 3 and 4) of the system suggest that mutualism can evolve easily from a state of free-living (\mathbf{a}_1,p_2 ; "never enter", "non-demanding"). If the system originates from parasitism (\mathbf{a}_4,p_2 ; "always enter", "non-demanding"), it can initially drift to an intermediate frequency of conditional agents and all

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